

Fish can shrink under harsh living conditions

Ari Huusko^{*1}, Aki Mäki-Petäys², Morten Stickler³ and Heikki Mykrä⁴

¹Finnish Game and Fisheries Research Institute, Kainuu Fisheries Research, Manamansalontie 90, 88300 Paltamo, Finland; ²Finnish Game and Fisheries Research Institute, Oulu Game and Fisheries Research, Tutkijantie 2 E, 90570 Oulu, Finland; ³Statkraft AS, Environmental Corporate Staff HSE, Lilleakerveien 6, 0216 Oslo, Norway; and ⁴Finnish Environment Institute, P.O. Box 413, 90014 University of Oulu, 90014 Oulu, Finland

Summary

1. Growth of the body length in vertebrates is well known to be unidirectional, with organisms progressively increasing in body size as they become older. However, there is evidence that body length shrinkage is a survival strategy for some vertebrates under unfavourable environmental conditions. Here we report both experimental and field evidence that the body length of young stream-dwelling salmonids can decrease in winter.

2. In examining how juvenile salmonid fish responded to harsh environmental conditions, we were faced with unexpected and previously undocumented observations in terms of growth performance, indicating that fish do shrink in harsh winter conditions. Young salmonids showed significant shrinking of individual body length, up to 10% of the body length, over the course of winter. The dynamics of the growth in length of these fish can be explained by a combination of anorectic stress and environmental conditions. Under stable, sheltered underwater conditions fish were best able to maintain positive growth in length.

3. We propose that growth in body length of a vertebrate animal can be temporally negative, individuals suffering from nutritional deficits shrinking in their length in addition to losing their body mass. There is circumstantial evidence that subsequent compensatory growth can have unexpected and dramatic longer-term costs. Experimental approaches, both field- and laboratory based, are sorely needed to reveal how common a phenomenon negative structural growth is among animals, and what the consequences are for individual performance, and, furthermore, for population dynamics.

Key-words: growth, length, shrinkage, fish, salmonids, winter

Introduction

Surviving harsh environmental conditions is challenging for both terrestrial and aquatic animals. Many animals experience either predictable or unpredictable and sometimes prolonged periods of food shortage, or periods when engaged in other activities that compete with feeding (Mrosovsky & Sherry 1980). Loss of body mass during such periods is a well-known phenomenon (Mrosovsky & Sherry 1980; Metcalfe & Thorpe 1992; Hodges, Boonstra & Krebs 2006), but associate changes in body length are rarely reported (Dehnel 1949; Saure & Hyvärinen 1965; Hofmann, Benson & Fernald 1999). Small mammals, such as insectivorous shrews, show body length shrinkage of up to 7%, and loss of mass of up to 35% in early winter, termed Dehnel's phenomenon (Dehnel 1949; Saure & Hyvärinen 1965). On the other hand, marine iguanas, ectothermic lizards living in the

Galapagos archipelago, shrink as much as 20% of their body length over the years of El Nino events when food availability dramatically decreases due to considerable temperature increase (Wikelski & Thom 2000). Both of these growth patterns are considered to be adaptive responses to harsh environment and energetic stress.

In northern latitudes, winter provides a template against which strong natural selection may occur, with only those individuals best able to obtain and allocate resources surviving to the subsequent growing season (Huusko *et al.* 2007). Here we report on the covariation between a harsh winter environment and growth in juvenile salmonids. The results originate from two environmental experiments, carried out in semi-natural stream channels in Finland, using Passive Integrated Transponder (PIT)-tagged hatchery-raised brown trout *Salmo trutta* L. (Fig. 1), to test for the effects of manipulated stream bed structure and ice cover conditions on over-winter performance of these fish. In addition, to reveal the growth dynamics in a hostile natural environment, we

*Correspondence author. E-mail: ari.huusko@rktl.fi



Fig. 1. A juvenile brown trout dwelling in the bottom of a pool in one of the experimental streams at the Finnish Game and Fisheries Research Institute's research station.

analysed a comparable field data set on wild Atlantic salmon *Salmo salar* L. individuals over-wintering in a small river in north-eastern Newfoundland, Canada.

Materials and methods

EXPERIMENTAL PROTOCOLS

To monitor salmonid fish growth dynamics in winter conditions, we conducted two experiments in parallel semi-natural stream channels in the Finnish Game and Fisheries Research Institute's research station in Paltamo, northern Finland (64°N, 27°E). The channels are 25.5-m long and 1.5-m wide (Vehanen 2006). The channel walls are made of concrete, but the stream bed is constructed of natural materials, such as gravel, cobbles and boulders. For these studies, a 10–15 cm layer of coarse gravel/pebble (20–35 mm in diameter) was placed onto the channel bed, which had a gradient of 0.3%. All six channels share the same water source, so the temperature regime was also the same in all the experimental units.

In the first experiment, conducted during 16 November 2001–19 February 2002, three out of six channels were randomly selected and constructed to mimic simplified (channelized) streams (SS), whereas three other channels mimicked natural streams (NS) with a heterogeneous bed structure. A similar amount of cobble-to-boulder sized stones (> 128 mm in diameter) were added to each channel, but with differing spatial arrangement. In the NS, stones were placed across the channel bed, often clustered perpendicular to the flow, resembling the weirs and deflectors of natural streams. Furthermore, areas between stone clusters were slightly deepened, resulting in a variable longitudinal channel profile with a distinct riffle-pool structure typical of natural streams (Nilsson *et al.* 2005). Stones in the SS were placed along channel margins, leaving the mid section open. The mid section was further canalized to have a v-shaped cross-section and smooth longitudinal bed elevation. We recorded water depth (cm), mean water column velocity (cm s^{-1} at $0.6 \times \text{depth}$) and dominant substratum size (modified Wentworth scale; mud or silt < 0.07 mm, sand 0.07–2 mm, gravel 216 mm, pebble 16–64 mm, small cobble 64–128 mm, large cobble 128–256 mm and boulders > 256 mm) at seven points in 25 cross-sectional transects placed 1 m apart. Average values of water depth and mean water velocity differed little between

the treatments [natural streams, depth 12.2 ± 6.9 cm (mean \pm 1SD), current velocity 22.2 ± 19.6 cm s^{-1} ; channelized streams, depth 10.7 ± 7.1 cm, current velocity 21.8 ± 21.1 cm s^{-1}]. However, the spatial configuration of stream habitat differed strongly among the channel types.

We introduced 40 age-0 (total length 94 ± 1.42 mm, mass 8.5 ± 0.41 g) and 10 age-1 (length 180 ± 6.42 mm, mass 58.5 ± 6.51 g) (means \pm 1SE) brown trout to each channel in 16 November 2001. The fish total length, i.e. the length from the snout to the tips of the tail fin of the fish (measured to the nearest mm), and mass were measured under anaesthesia (with MS-222) in standard laboratory conditions, using the same measuring rule and scale in every measurement trial. The fish used were hatchery-raised brown trout of the River Oulujoki strain, derived from second-generation brood stock established in the early 1990s from several local brown trout stocks of the River Oulujoki watercourse. In the hatchery, the fish were reared in circular plastic tanks (3.5 m²; water depth 30 cm, discharge 0.45 l s^{-1}) at the average density of 3 kg m^{-2} . The fish were fed on commercial dry pellet feed (Nutra Parr 1.5 mm, Skretting, Norway; total energy content 22 kJ g^{-1} , protein 51%, lipid 21%), with the daily feed, 0.2% of the total fish mass in each tank, being distributed by automated feeders evenly during daylight hours.

Before introduction to the channels, fish were individually PIT-tagged (tag model ID100, size 11.5×2.1 mm; Trovan Ltd, Douglas, UK). The tag was injected into the body cavity under anaesthesia at the same time as the fish length and mass measurements were carried out. Fish density in the channels (1.3 ind. m^{-2}) was well within the range of densities of juvenile brown trout in streams of northern Finland (Korsu, Huusko & Muotka 2007). At the end of the experiment, fish were sampled using one-pass electrofishing, yielding 175 individuals in total (27, 25 and 33 individuals from NS-treatments, 29, 33 and 28 individuals from SS-treatments), and each fish captured was identified for its PIT-code and measured for total length and mass without knowledge of previous body length and mass. The channels supported benthic invertebrate communities very similar to those in a nearby river in terms of species composition and total density (Korsu, Huusko & Muotka 2009). Thus, there was no need to provide additional feed for the fish. The water temperature during the experiment was stable (mean \pm 1SD: 1.4 ± 0.1 °C). All channels also received a similar discharge regime (mean \pm 1SD: $20.8 \pm 4.4 \text{ l s}^{-1}$).

In the second experiment conducted during 5 January 2005–24 March 2005, we used three of the six channels used in the first experiment, each channel divided in three sections by wire mesh (mesh size 10 mm). The channel bed was modified so that each section comprised an upstream riffle (water velocity $20\text{--}60 \text{ cm s}^{-1}$, depth 15–25 cm, mean substrate diameter 15 cm) and a downstream pool section ($0\text{--}20 \text{ cm s}^{-1}$, 25–35 cm, 4 cm respectively). Hence, we had nine similar sections, where we performed three treatments: an open channel treatment, a half-open channel with simulated ice cover by covering the pool section of the channel, and a closed channel with simulated ice cover over the whole treatment arena. We ran three replicates for each treatment in randomly selected sections. Before 10 age-1 (total length 147 ± 1.9 mm, mass 36.2 ± 1.4 g) (means \pm 1SE) brown trout (0.78 ind. m^{-2}) were introduced to each of the experimental arenas, we anaesthetized (MS-222) them, measured for total length and mass, and injected their body cavities with PIT-tags (tag length; 23 mm; diameter; 3.9 mm; weight: 0.6 g in air, Texas Instruments Ltd, Dallas, TX, USA) to obtain individual-level data. The total length and mass measurements were carried out identically to the procedure described in connection with the first experiment. The channels supported benthic invertebrate communities very similar to those in a nearby river in terms of species composition and total

density (Korsu, Huusko & Muotka 2009). Therefore, we did not feed the fish during the experiment. At the end of the experiment, fish were sampled using electrofishing, and each fish was identified for PIT-code and measured for total length and mass without knowledge of previous body length and mass. Water temperature during the experiment was stable (mean \pm 1SD: 1.6 ± 0.1 °C).

We used repeated measure analysis of variance (rmANOVA) with Greenhouse-Geisser corrected degrees of freedom to test for the effects of treatment on the growth of over wintering trout. We analysed the data both in absolute terms and by proportional change, resulting in identical patterns, so we have presented absolute change in this paper. The growth in length of a fish on each consecutive time was the within-subject factor (time) and treatment was the between-subject factor. To account for possible variation among our experimental channels, we also tested for the effect of channel nested within the treatment, but interaction with time for this term was not statistically significant ($F < 0.791$, $P > 0.533$, d.f. = 4, 117 for age 0+ and 4, 49 for age 1+ fish in experiment 1, and $F = 0.826$, $P = 0.553$, d.f. = 6, 81 in experiment 2) and it was dropped from the final models. Separate analyses were conducted for both age groups of the first experiment. All analyses were performed on untransformed data, because homoscedasticity and normality assumptions were always met.

FIELD STUDY

Growth of over wintering wild Atlantic salmon parr were studied in the Southwest Brook, a small, natural river located in Terra Nova National Park ($48^{\circ}36'25''\text{N}$, $53^{\circ}58'50''\text{W}$) on the north-east coast of Newfoundland, Canada. The river has a catchment area of 36.7 km^2 with an average gradient of 1.3%. Mean winter discharge is $0.4 \text{ m}^3 \text{ s}^{-1}$. The study section is considered as fast flowing with few pools. Boulders and cobbles form the dominant material of the streambed substrate. During winter the river is very heavily impacted by dynamic ice formation, showing repeated anchor and frazil ice events (Stickler *et al.* 2008).

From 24 to 25 November 2005 (water temperature 6.0 °C) a total of 145 Atlantic salmon parr [mean \pm SD, fork length (i.e. the length from the snout to the tips of the shortest fins in the middle of the tail fin) 12.6 ± 1.6 cm, body mass 20.5 ± 7.2 g] were caught using a 24 V backpack electrofisher (Model 12, Smith-Root Inc., Vancouver, WA, USA). Each individual was surgically implanted with PIT-tag (Texas Instruments; length 23 mm, diameter 3.9 mm, weigh: 0.6 g in air, tag/fish weight ratio min. 0.9%, max. 5.7%). For tagging and measuring, fish were anesthetized by immersion in an aqueous solution of clove oil (100 ppm). After surgery, fish were then kept for 24 h before releasing them into their respective habitats in the river. In spring (between 28 April and 15 May 2006), study section was sampled by electrofishing to recapture tagged parr. Fish caught ($N = 31$) were measured by fork length and body mass without knowledge of previous body length and mass. The growth in length of the fish over the winter was analysed by paired *t*-test.

Results

Our first experiment demonstrated significant shrinking of individual body length among two age-groups of young hatchery-raised brown trout in the course of winter (rmANOVA: $F > 31.804$, $P < 0.001$, d.f. = 1, 121 for age 0+ and 1, 53 for age 1+ aged fish respectively). Typically, the majority of individuals in each experimental unit decreased in length,

with some individuals shrinking as much as 10 mm (almost 10%) of their body length, while some, in fact, gained body length during the same time period (Fig. 2a,b). The configuration of the stream bed structures did not affect body length

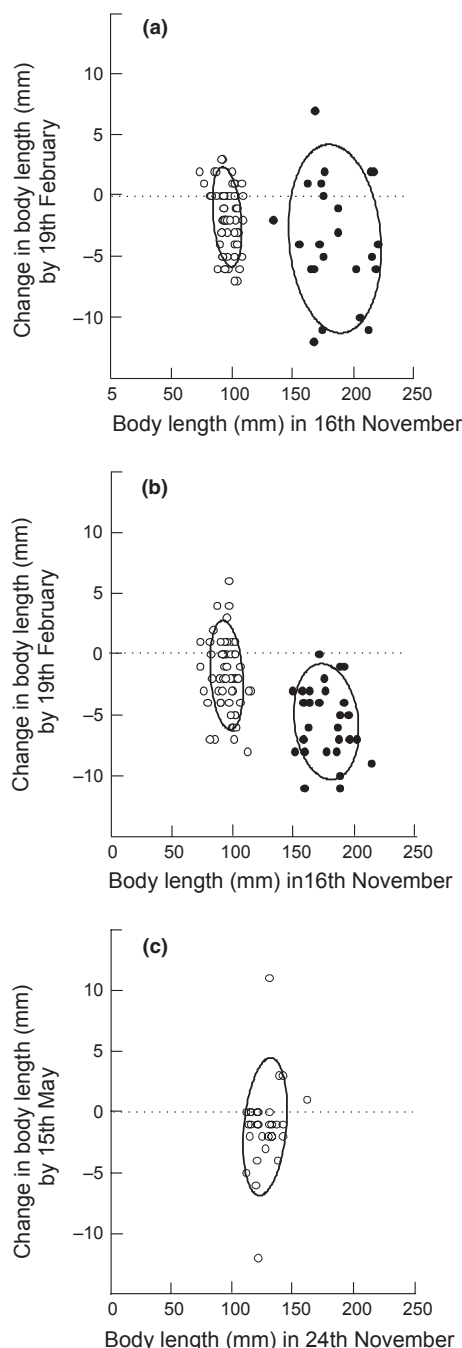


Fig. 2. Changes in the total body length (mm, from the initial length) of young salmonids during winter. a and b: experimental design with young-of-year (open dots) and 1-year-old (black dots) brown trout in natural-like stream channels (a), and simplified stream channels (b). c: young Atlantic salmon in Southwest Brook, a natural stream in Canada. The ellipses are centred on the sample means of the *x* and *y* variables. The unbiased sample standard deviations of *x* and *y* determine the major axes of, and the sample covariance between *x* and *y* the orientation of the ellipses. The dot line indicates no change in length.

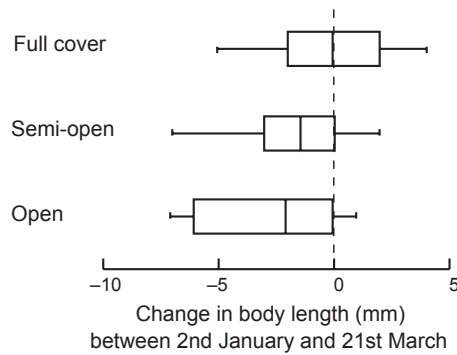


Fig. 3. Change in the total body length of 1-year-old brown trout living in experimental streams. All streams had riffle-pool sections with one of the treatments used: fully simulated ice-cover (Full cover), partial simulated ice-cover (Semi-open) and no ice-cover (Open). Boxes represent 50% of the observations, with median value indicated by a line, whiskers indicate 90% of data range. The dot line indicates no change.

dynamics (rmANOVA: $F = 0.256, 0.139, P = 0.614, 0.711$, d.f. = 1, 121 and 1, 53 for 0+ and 1+ aged fish respectively). Although there was no correlation within each of the two age-groups of brown trout between the initial size of fish and the shrinkage, fish in the older age group shrank more during winter. Thus, the negative growth in length was length-dependent [linear regression on data pooled over treatments and age-groups: $\text{growth (mm)} = -0.028 L_{\text{start (mm)}} + 0.822$, $P < 0.001$]. The fish that decreased in body length also decreased their mass. Among young-of-year trout there was no clear pattern between these two characteristics (Pearson correlation on data pooled over treatments: $P = 0.408$), but 1-year-old trout lost more mass the more their length decreased (Pearson correlation on data pooled over treatments: $P = 0.010$). The experimental evidence on the body length shrinkage was further supported by the results from the field study on young Atlantic salmon in a river facing extremely harsh environmental conditions due to highly variable ice dynamics in winter (Stickler *et al.* 2008). The majority of young salmon were shorter in spring compared to their autumn size although this difference only bordered on statistical significance (paired *t*-test: $P = 0.078$; Fig. 2c).

The second experiment showed that shrinkage frequency increased along the environmental complexity gradient. Fish dwelling in open riffles shrank more than fish in comparable streams with overhead cover (rmANOVA: time effect: $F = 35.053, P < 0.001$, d.f. = 1, 87; time*treatment interaction term: $F = 7.345, P = 0.001$, d.f. = 2, 87, Fig. 3). Considering the results of our first experiment, the overhead cover, unlike stream bed cover as such, appeared to be vital for overwintering trout.

The observed shrinkage in young fish could be an artefact based on measurement errors. To control for possible measurement errors the research fellow responsible for fish measurements in our experiments was subjected to a test where 50 one-year-old individually tagged brown trout were measured three times using the same measurement procedure as described in the methods, and without knowledge of previous

body length. Mean intra-individual measurement error in length was 0.56 (SD = 0.65) mm [being equal to 1.00 (SD = 0.45) % of body length]. This reveals that the observed negative growth of the young salmonids, being clearly greater than possible measurement error (Figs 2 and 3), was a real phenomenon and not an artefact.

On the other hand, there are numerous studies in literature demonstrating fish length shrinkage after death or if preserved in a solution of preservatives or deep frozen (Shetter 1936; Morison 2004). Young Atlantic salmon become, on average, 10% shorter when frozen compared to their original length (Armstrong & Steward 1997). The shrinkage of live fish, both the brown trout in our experiments and the natural salmon in the field conditions, was, on average, smaller compared to frozen young salmon (Armstrong & Steward 1997), indicating that shrinkage of live fish was somehow controlled by the physiological processes in soft tissues of fish themselves.

Discussion

In winter, young wild salmonids tend to be found in cavities under stones in the stream bed, spending the majority of their time hidden and being relatively quiescent, sheltering from energy demanding environmental conditions, and avoiding risks of being preyed on by active predators e.g. by only feeding during the hours of darkness (Huusko *et al.* 2007). These fish use stored lipid, deposited during preceding summer, as an energy source and normally exhibit a gradual depletion of storage energy reserves during the winter. It has been suggested that young salmonids enter a state of over-winter anorexia, concomitant with highly weakened (up to 96%) appetite, during autumnal transition period (Metcalf & Thorpe 1992). However, the degree and duration of anorexia in overwintering salmonids is regulated by energy reserves so that the fish effectively having a defended energy level below which appetite and activity is temporarily increased until lost energy reserves have been restored (Metcalf & Thorpe 1992). Further, the standard metabolic rate of over-wintering fish is found to be a function of habitat structure, with the presence of appropriate shelters providing metabolic benefit to fish (Millidine, Armstrong & Metcalf 2006; Finstad *et al.* 2007). These behavioural adaptations may partly explain why body shrinkage of salmonids is not observed in relatively benign field conditions (Parrish, Hawes & Whalen 2004; Huusko *et al.* 2007).

We used hatchery-raised fish in our experiments. Hatchery-raised salmonids released to natural environment in autumn show significantly smaller food intake and slower growth than wild congeners (Ersbak & Haase 1983; Shurov, Smirnov & Shustov 1987; Vehanen, Huusko & Hokki 2009). Low feeding efficiency on wild prey in autumn can therefore prevent hatchery-raised fish from building up lipid reserves, which could indicate stronger anorexia resulting in body shrinkage. On the other hand, young wild salmon in Southwest Brook may have faced an analogous situation due to ice conditions limiting access to feeding. Under adverse environment fish

may have to, after exhausting the lipid reserves, reabsorb other body tissues, leading to a shortening of the body length. Further, it may well be that after lipid stores or other energy reserves have been utilized (Biro *et al.* 2004; Nasje *et al.* 2006), there is a certain individual-based limit to the amount an animal can endure and resorb energy from the body components, with death following when the limit is overdrawn (Finstad *et al.* 2004). In fact, body shrinkage of fish and lizards is involved in low population survival. Iguanas show high mortality, of up to 90% of a population, during the periods when body shrinkage is observed (Wikelski & Thom 2000). For salmonids, winter is considered a bottleneck period with considerable mortality (Huusko *et al.* 2007). On the other hand, shrews going through the Dehnel's phenomenon annually show no correlation between shrinkage and winter severity or survival (Hyvärinen 1965, 1994; Henttonen *et al.* 1989), revealing that body size shrinkage promotes winter-time performance. These contrary facts indicate that body shrinkage of ectothermic fish and lizards can be regulated more by starvation and environmental forcing than the mechanisms taking place annually in endothermic shrews (Dehnel 1949; Saure & Hyvärinen 1965).

The key characteristics of body shrinkage of the salmonids observed here have still analogous characteristics of shrinkage reported for shrews, and even for humans suffering from anorexia or malnutrition in general (Wikelski & Thom 2000). Negative structural growth calls for changes either in bone metabolism and/or bone structures or in soft tissues, or in both of these. However, there are no detailed studies on the exact mechanisms leading to a shorter body size of fish or lizards. It has been suggested that there may be a causal relationship between anorexia, limited exercise and high corticosterone levels (indicating stress) and decreases in body length of iguanas (Wikelski & Thom 2000). In shrews, reduced body size in autumn/early winter is caused mainly by decreasing the volume of the nuclei pulposi in the vertebral discs of the spinal column (Hyvärinen 1965; Saure & Hyvärinen 1965). This leads to flattening of these formations and thus into the shortening of the spinal column, and hence body length. If, as in shrews, the nucleus pulposus in the vertebral discs of the spinal column shrink c. 0.08 mm each (Hyvärinen 1965), then based on the number of vertebrae of salmonids (55–60) fish could shrink about 4–5 mm, which approximates with the observations reported here (Fig. 1).

Growing animals are often able to offset the effects of periods of reduced food availability, and subsequent changes in body size, but a period of anorexia with mass loss and subsequent compensatory growth can have unexpected and dramatic longer-term costs (Morgan & Metcalfe 2001; Johnsson & Bohlin 2006). Juvenile salmon subjected to a short-term low-food regime in autumn subsequently entered a hyperphagic phase, leading to complete restoration of lipid reserves and a partial recovery of lost growth relative to controls (Morgan & Metcalfe 2001). However, several months later they entered a prolonged phase of poorer performance, so that by the following spring they were substantially smaller

than controls and had lower lipid reserves for their body size (Morgan & Metcalfe 2001). Juvenile brown trout, suffering food deprivation and mass loss in spring, showed delayed mortality 10 months later, apparently induced by the compensatory responses (Johnsson & Bohlin 2006). Further, shrews, going through the body shrinkage during their first autumn/early winter, start growing in the following spring, but are short-lived, dying before next winter (Hyvärinen 1965, 1994). These observations provide circumstantial evidence that when shrinkage in length, accompanied with mass loss, is experienced, the consequences of the following catch up growth most probably will later have even strengthened impacts compared to mere mass loss. Our experiments reveal that hatchery-raised salmonids are very susceptible to shrink under harsh riverine conditions, indicating poor performance later. There is a great need to find ways to improve the performance of such fish when used for supplementation of endangered wild populations, a relatively common practice used in fisheries conservation and management.

Taken together, to understand seasonal variations in body size of animals, one must consider many aspects of nutritional ecology and animal energetics as well as trophic interactions and life history trade-offs. So far there are only very few observations indicating body length shrinkage (individual level data: Dehnel 1949; Hofmann, Benson & Fernald 1999; Wikelski & Thom 2000; this study, population level data: Ikeda & Dixon 1982; Marinovic & Mangel 1999), and the generality of the phenomenon is unknown. However, growth rates should no longer be set to zero, as shrinkage can confer biologically important advantages or cause more trouble than it's worth. Experimental approaches, both field- and laboratory based, are sorely needed to reveal how common a phenomenon body shrinkage is among animals, and what are the consequences for individual performance, and, furthermore, to population dynamics.

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